Evidence for natural hybridisation in hermit hummingbirds (*Phaethornis* spp.)

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Hybridisation occurs infrequently, though regularly, in hummingbirds (Gray 1958, Banks & Johnson 1961, Short & Phillips 1966, Graves 1990). In the Trochilidae, hybrids have often caused taxonomic problems and the erection of new species or even genera (for details, e.g., Meyer de Schauensee 1947, 1966, Berlioz 1929, 1932, 1938, 1964, Berlioz & Jouanin 1944, Graves 1990, Graves & Zusi 1990, Hinkelmann *et al.* 1991). Species with similar habitat requirements and mainly allopatric distributions may hybridise where they meet in contact zones. Others, with different habitat preferences, may interbreed where their favourite environments have a common border.

Until now, hybrids between hummingbird species have been reported only from the larger of the two subfamilies, the Trochilinae. Sibley (1957) recognised the importance of visual signals, e.g. nuptial flight or iridescent plumage, in the contact between the sexes and the display behaviour of trochiline hummingbirds. He reported 37 hybrid combinations, with 28 genera involved. Of these, 21 are sexually dimorphic; only in 7 cases are the sexes alike.

In hermit hummingbirds of the subfamily Phaethornithinae, the species are almost or totally sexually monomorphic, and plumage characters are not strongly specific. In their display behaviour, vocalisation appears to be more important than visual signals. Graves & Zusi (1990) recently confirmed that there are no reports of hybrids in which one parent species belongs to the Phaethornithinae, nor did they cite any case of hybridisation within the hermit subfamily.

In the course of examining over 4200 study skins of *Phaethornis* specimens from all parts of their respective distributions, I discovered 7 specimens that could not be assigned without hesitation to the many taxa described within the genus. Previous authors had also noticed that linear measurements and plumage colourations of 3 of these specimens did not agree with the variation found in the established taxa, and these 3 specimens were thus used to describe two new subspecies of the polytypic and widely distributed *Phaethornis longuemareus* (Zimmer 1950, Phelps & Phelps 1952). For 6 of the 7 specimens there were exact collecting localities; in one case the locality was not exactly known, but near a large city. Careful comparisons with regard to the examination advice by Graves (1990) revealed that each of the 7 specimens exhibited intermediate characters between two different species occurring in the same area. Based on the probability of a mosaic expression of parental autapomorphies (Graves 1990) in plumage characters and linear measurements (Table 1), a hybrid origin may thus be the most likely explanation.

TABLE 1
Linear measurements (mm) of probable hybrid specimens and their parental taxa in the genus *Phaethornis*

	Parental species 1				Parental species 2		
	n	mean	range	Probable hybrid	*n*	mean	range
		P. r. ruber		ZFMK 1982/46		*P. stuarti*	
bill, ♂	52	22.9	21–25	22	16	23.5	23–25
wing, ♂	56	30.3	28–34	36	16	39.6	37–41
		P. r. ruber		AMNH 285949		*P. rupurumii amazonicus*	
bill, ♂	52	22.9	21–25	26	21	25.8	24–27
wing, ♂	56	30.3	28–34	42	22	45.5	44–47
				AMNH 285951			
bill, ♀	98	23.1	21–25	25	14	25.8	24–27
				CMNH 74518			
				26			
				AMNH 285951			
wing, ♀	105	34.8	32–37	42	14	44.8	43–47
				CMNH 74518			
				43			
		P. r. rupurumii		Phelps 17728		*P. longuemareus*	
bill, ♂	20	25.7	25–27	27	38	25.5	24–27
wing, ♂	22	44.3	41–46	44	40	42.8	41–44.5
				MCZ 95863			
bill, ♀	15	25.8	25–28	(broken)	41	25.3	23–27
wing, ♀	15	44.5	42–46.5	45	42	43.2	41–45
		P. s. superciliosus		AMNH 233750		*P. m. malaris*	
bill, ♀	38	36.0	33–39	40	17	44.1	42–46
wing, ♀	42	56.8	55–58	60	16	64.5	62–66.5

Phaethornis ruber ruber x *P. stuarti*

A single specimen caught in the vicinity of Cochabamba, Bolivia, arrived alive in Germany in 1981. It was purchased by Dr Karl-L. Schuchmann and, after it died, was deposited in the scientific collection of the Zoological Research Institute and Museum Alexander Koenig (ZFMK) in Bonn (♂, ZFMK No. 1982/46, coll. by Charles Cordier, October 1981, "Cochabamba"). Whereas linear measurements (Table 1), in particular wing-length, are intermediate between *Phaethornis ruber ruber* and *P. stuarti*, plumage colouration provides few clues. The reddish belly is paler than in nominate *ruber* and agrees with *stuarti*, the breast is more intensely coloured than in *stuarti* and equals *ruber*, the whitish chin area is as small as in *ruber* and smaller than in *stuarti*. The margins of the four outer pairs of rectrices are whitish as in adult *stuarti* (reddish in *ruber*), and the whitish tip of the central pair of rectrices is as small as in *ruber* and thus smaller than in *stuarti*.

However, *Phaethornis ruber* and *P. stuarti* are sister species and can be distinguished only by a few slight differences in plumage colouration. Nominate *ruber* and *stuarti* approach each other in S.E.

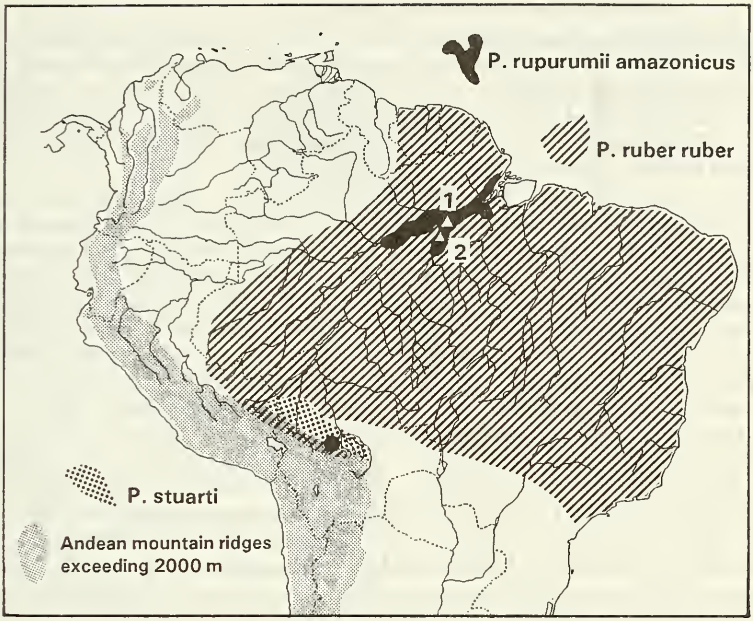

Figure 1. Distributions of *Phaethornis ruber ruber*, *Phaethornis stuarti*, and *Phaethornis rupurumii amazonicus* (range within the distribution of *P. r. ruber*). Black dot: Cochabamba, Bolivia; white triangles: 1—Santarem, Brazil, 2—Caxiricatuba, Brazil.

Peru and W. Bolivia (Fig. 1) and behave almost exclusively like paraspecies. Their only sympatric distribution is in the southern part of the Departamento Madre de Díos, Peru, but this population of *stuarti* may be isolated.

Although both species are known from sea level to 1000 m, in the contact area along the Eastern Andes on the upper course of the Beni river northeast of Lake Titicaca *P. stuarti* mainly inhabits the lowlands whereas *P. r. ruber* is limited to higher elevations. The bird in question very probably originated from the Yungas or Chapare region north of Cochabamba where nominate *ruber* and *stuarti* are in contact, and no other *Phaethornis* species of similar body mass is found.

Phaethornis ruber ruber x *P. rupurumii amazonicus*

In 1950, Zimmer described two birds, male and female, from Caxiricatuba, on the right bank of the lower Tapajos river (Fig. 1), as "*Phaethornis longuemareus aethopyga*". Due to the intensely dark-coloured throat he considered the new form to belong to the polytypic *P. longuemareus*, a species widely distributed between S. Mexico and central Peru, in N.E. South America and in Trinidad. The description of *aethopyga* apparently extended the species' distribution to the lower Amazons.

Careful examination of their morphological characters, however, has revealed that the taxa comprising *Phaethornis longuemareus sensu* Peters (1945) represent a paraphyletic "species" which should be divided into three species; *longuemareus* (Trinidad, E. Venezuela to French Guiana), *atrimentalis* (east of the Andes from central Colombia to central Peru) and *striigularis* (S. Mexico to Venezuela and Ecuador west of the Andes) (Hinkelmann 1988a, 1990).

There are only two small *Phaethornis*, of similar size and body mass as *aethopyga*, occurring along the lower Amazons: *P. ruber ruber* and *P. rupurumii amazonicus*. Previous claims that *P. nattereri* is distributed in the campos 'islands' within *terra firme* forest along the lower courses of the rivers Amazons and Tapajos (Müller 1973, Hinkelmann 1988b; my map in Sick 1993, p. 342) are based on a misidentification by Pinto (1938). He later determined the unique specimen from Obidos correctly as belonging to the subspecies *amazonicus* which he considered, like *rupurumii*, to belong to *P. squalidus* (Pinto 1947).

Three specimens of *aethopyga* are preserved in scientific collections (American Museum of Natural History, New York: ♂, AMNH No. 285949, Caxiricatuba, Brazil, coll. A. M. Olalla, 20 May 1931, type specimen; ♀, AMNH No. 285951, Caxiricatuba, coll. A. M. Olalla, 9 May 1931; Carnegie Museum of Natural History, Pittsburgh: ♀, CMNH No. 74518, Colonia de Mojuj, Santarem, Brazil, coll. S. M. Klages, 27 October 1919). Both localities are located on the right bank of the lower Tapajos river, south of the Amazons.

Careful examination of these specimens revealed that their morphological characters are intermediate between *P. ruber ruber* and *P. rupurumii amazonicus* or agree with those of either probable parental species. The male (AMNH No. 285949), portrayed in Grantsau (1988, p. 149), agrees with nominate *ruber* in the colouration of the chin, breast, belly, upper and under tail-coverts, and margins of the rectrices, and the more intense iridescence of the upperparts. Dark throat colouration, breadth of the margins of the rectrices, and bill length correspond to *amazonicus*. Intermediate characters are the shape of the rectrices and the general size as expressed, e.g., by wing-length (Table 1). White colouration at the base of the outer rectrices is due to a (possibly individual) lack of pigments and is missing in both probable parental species.

The female specimens are very similar to each other, the only difference being more greyish underparts in CMNH No. 74518. Whereas the greyish colour very much resembles *amazonicus*, the more reddish underparts of AMNH No. 285951 are very similar to those of *ruber*. Chin, breast, belly, upperparts, upper and under tail-coverts agree with the male specimen and, together with intermediate measurements, point to the probable hybrid origin. The participation of *amazonicus* is corroborated by the darkish throats of each of the three specimens. The rachis of the central pair of rectrices is red, which clearly indicates the parenthood of *ruber* because this character state is synapomorphic in *P. ruber* and its sibling, *P. stuarti*.

Phaethornis ruber inhabits lowland rain forest as well as several types of more open and drier forests. In the lower Amazons region it also

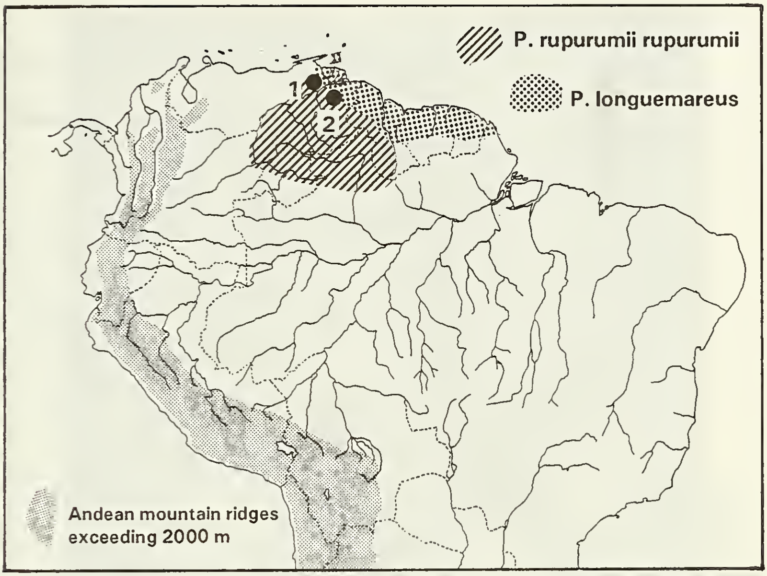

Figure 2. Distribution of *Phaethornis rupurumii rupurumii* and *Phaethornis longuemareus*. Black dots: 1—Monagas, Venezuela, 2—Cerro Tomasote, Venezuela.

occurs in the *várzea*, in secondary forests and the *campos* islands (Snethlage 1908, 1913, 1928, Stone 1928, Peres & Whittaker 1991). The latter habitat types are preferred by *P. rupurumii amazonicus*, which is lacking in forest of the *terra firme* (Snethlage 1913). Caxiricatuba and Santarem are both located in the area of *campos* islands.

Phaethornis rupurumii rupurumii x *Phaethornis longuemareus*

The nominate subspecies of *Phaethornis rupurumii* and the closely related *P. longuemareus*, which should be regarded as a monotypic species (Hinkelmann 1988a, 1990), meet each other in N.E. Venezuela and W. Guyana (Fig. 2). Two specimens exhibiting characters of both species are preserved in scientific collections (Phelps Coll. No. 17728, deposited in the AMNH, New York: ♂, Cerro Tomasote, El Palmar, Bolívar, Venezuela, coll. Fulvio Benedetti, 6 April 1942; Museum of Comparative Zoology, Cambridge: MCZ No. 95863, ♀, Maturín, Monagas, Venezuela, formerly Coll. R. H. Jung, purchased by Barbour at Schlüter Co., Halle, Germany, in 1906). In 1952, Phelps & Phelps based the description of a new subspecies, *imatacae*, of the polytypic *P. longuemareus*, *sensu* Peters (1945), on the male from Cerro Tomasote. It is still the only known individual of this "subspecies" (Aveledo *in litt.*).

Linear measurements of both *P. rupurumii rupurumii* and *P. longuemareus* are very similar, and those of the probable hybrid specimens are within their regular range of variation (Table 1). Both

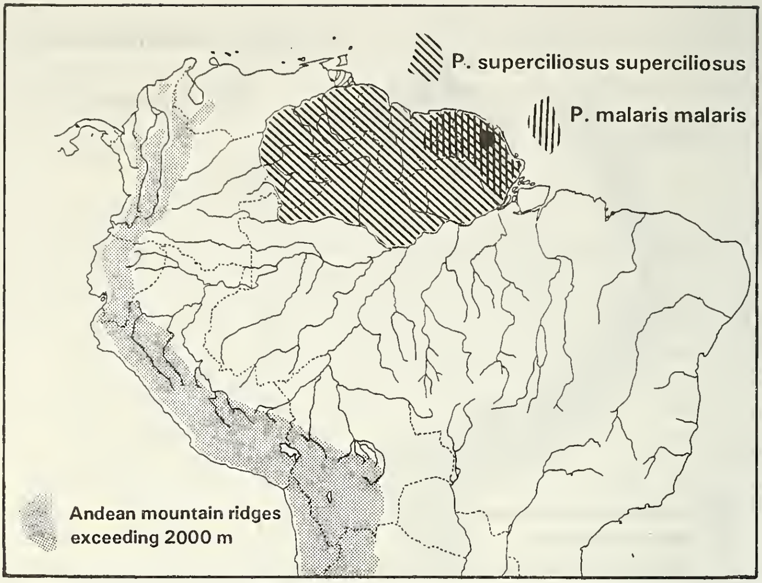
P. superciliosus superciliosus
P. malaris malaris
Andean mountain ridges exceeding 2000 m

Figure 3. Distribution of *Phaethornis malaris malaris* and *Phaethornis superciliosus superciliosus*. Black dot: Pied Saut, French Guiana.

specimens have dark throat-feathers with pale edges producing a striped appearance, as in *P. r. rupurumii*, whereas in *P. longuemareus* they lack pale edges so that the throat appears uniformly dark. The colouration of the sides of neck is ochraceous as in *longuemareus*, not brownish-grey as in nominate *rupurumii*; feather margins of the upper tail-coverts are rusty red as in *longuemareus*; those of *rupurumii* are ochraceous. The margins of the rectrices in the probable hybrid specimens show the usual sex difference (broader in females than in males) and are as narrow as in *P. rupurumii*; but these are even narrower in both sexes of *longuemareus*. The underparts of both specimens are brownish-ochraceous, intermediate between the orange ochraceous of *longuemareus* and the brownish-grey of *rupurumii*. The remaining parts of the plumage are similar in *P. longuemareus* and *P. r. rupurumii*.

The probable parental species prefer more open habitats to dense primary forests (with the exception of *P. longuemareus* in Trinidad where *P. ruber* is missing), such as semideciduous or mesophytic forest (*P. r. rupurumii*; Snyder 1966; Meyer de Schauensee & Phelps 1978) and swamp forest, secondary growth or forest edges (*P. longuemareus*; Phelps & Phelps 1958, Snyder 1966, Haverschmidt 1968). They behave like parapatric species but nothing is known about their possible strategies to avoid competition where both species meet. The two probable hybrids were collected in this area of probable contact (Fig. 2). The only other *Phaethornis* of similar body mass occurring in this

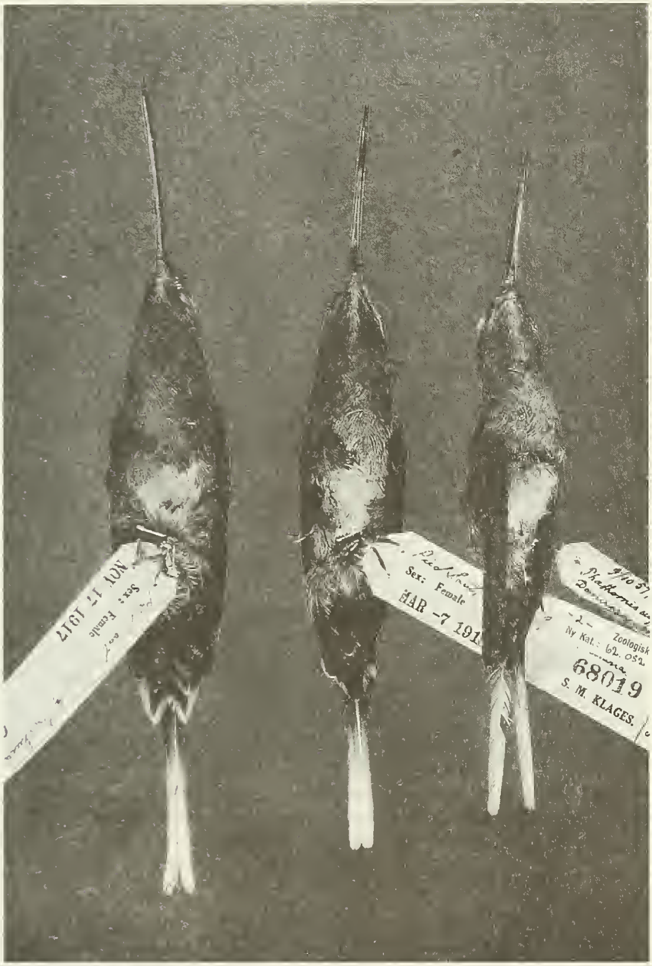

Figure 4. Ventral view of *Phaethornis malaris malaris* (left, Carnegie Museum of Natural History No. 64827, ♀), probable hybrid (centre, American Museum of Natural History No. 233750, ♀), and *Phaethornis superciliosus superciliosus* (right, Zoologisk Museum Copenhagen No. 62052, ♀). Photo: E. Schmitz.

region, *P. ruber episcopus*, inhabits wetter habitats like rain forests, is of smaller size, and easily distinguishable by plumage characters.

Phaethornis malaris malaris x *P. superciliosus superciliosus*

The *Phaethornis superciliosus-malaris-longirostris* species group consists of at least 14 valid subspecies distributed between S. Mexico and S.E. Brazil (Hinkelmann in press). There is only one region where two

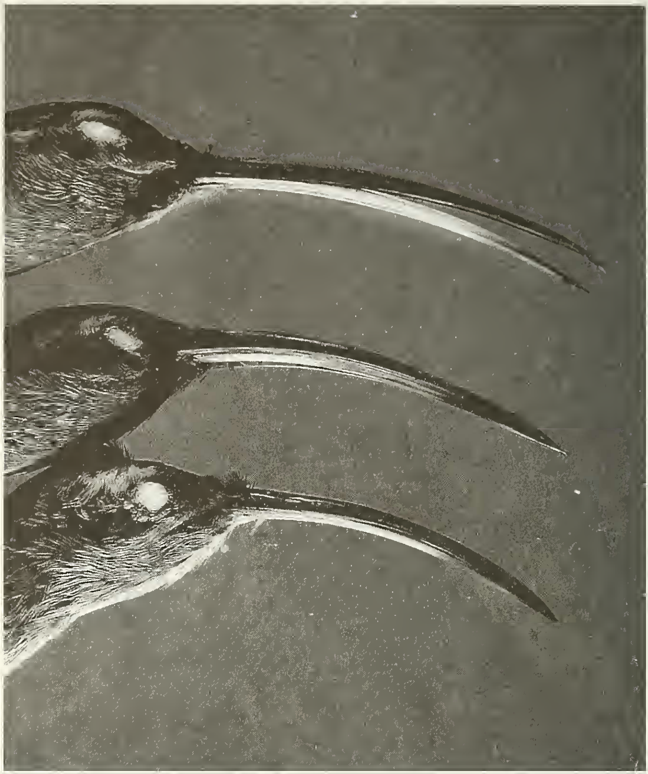

Figure 5. Heads of *Phaethornis malaris malaris* (above, ♀), probable hybrid (centre, ♀), and *Phaethornis superciliosus superciliosus* (below, ♀). The specimens are the same as in Fig. 4. Note the bill curvature. Photo: E. Schmitz.

members of the group occur in the same area: nominate *P. m. malaris* and *P. s. superciliosus* in Surinam, French Guiana, and the Brazilian state of Amapá (Fig. 3). The sympatric distribution of these closely-related taxa has made it difficult to define the species' limits, and it has been suggested that this is one of the few cases of "ring species" in ornithology (Peters 1945, Zimmer 1950).

Only one specimen is known which exhibits intermediate characters between *P. m. malaris* and *P. s. superciliosus* (New York: ♀, AMNH No. 233750, Pied Saut, Oiapoque, French Guiana, coll. S. M. Klages, 7 March 1918). *P. m. malaris* and *P. s. superciliosus* are easily distinguishable by size and colouration of the underparts (Fig. 4). The probable hybrid specimen is intermediate in linear measurements (Table 1) and plumage colouration. Female *P. s. superciliosus* have a prominent pale gular stripe whereas female *P. m. malaris* have only a small pale patch on the chin; the bird in question has a regular gular stripe, though narrower than in *superciliosus*. The remaining parts of its throat as well as its breast are as dark as in nominate *malaris*; they are paler in nominate *superciliosus*. The light ochraceous belly colouration of the probable hybrid is indistinguishable from *superciliosus*, but slightly deeper than in *malaris*. Its under tail-coverts are whitish with a dark base as in *superciliosus* (light ochraceous with dark base in *malaris*), whereas the margins of the rectrices are broader than in *superciliosus* and resemble *malaris*. The bill is more curved in *P. s. superciliosus* females than in *P. m. malaris* females; in the probable hybrid, it is intermediate (Fig. 5). In all remaining plumage characters, *P. s. superciliosus* and *P. m. malaris* do not differ.

Both probable parental taxa were collected by S. M. Klages 1917/18 at Pied Saut, French Guiana (e.g. *malaris*: Peabody Museum of Natural History, New Haven: PMNH Nos. 27754, 27755, 27757; New York: AMNH No. 233749; Pittsburgh; CMNH Nos. 64827, 67834, 68017; University of Michigan, Museum of Zoology, Ann Arbor: UMMZ No. 150093; *superciliosus*: PMNH No. 27753; CMNH Nos. 65672, 68005, 68104). They share the same habitat (Haverschmidt 1968, Mees 1977, Dick *et al.* 1984) and very probably use different feeding niches enabled by clearly different body masses (*P. m. malaris*: 7.5–10 g; *P. s. superciliosus*: 4–6.5 g), which are the most divergent within the *superciliosus-malaris-longirostris* species group. Whereas the body mass of *malaris* is unique in *Phaethornis*, there is one other congeneric species with a body mass very similar to *P. s. superciliosus* occurring in French Guiana and adjacent countries, *P. bourcieri*. This species, however, is morphologically clearly separated by its straight bill and a greyish-brown plumage.

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